from the sulphate of iodo-quinine, which, it may be remembered, contains 32·609 per cent. iodine and 10·61 per cent. sulphuric acid.

I hope soon to present these results in more detail when sufficient leisure is afforded me for the purpose.—W. B. H.

January 29, 1857.

Major-General SABINE, Treas. and V.P., in the Chair.

The following communications were read:—

I. "On the Nervous System of *Lumbricus terrestris*." By J. Lockhart Clarke, Esq., F.R.S. Received Dec. 18, 1856.

(Abstract.)

In the summer of 1855, with the view of throwing some light on other researches in human anatomy, in which he was already engaged, the author undertook some anatomical inquiries on the nervous system of Invertebrata; but finding them occupy more time than he could spare, he was compelled to relinquish the pursuit after having made many interesting but desultory observations on various animals. As he had proceeded, however, to a considerable extent with the nervous system of *Lumbricus terrestris*, and discovered in it much that is important and was hitherto unknown, he has thought it expedient to resume and complete this portion of the subject without further delay.

Before treating of the nervous system it was necessary,—in order to show the proper functions of many of its parts,—to give some account of the organs of prehension, deglutition and digestion; and as these are insufficiently explained elsewhere, the author has described them entirely from his own dissections and observation.

The first anterior segment is a conical or nipple-shaped projection inserted behind into the upper fifth of the second segment, or first ring. Its dorsal surface is covered, except in the centre, by concentric laminæ and irregular masses of pigment-granules, which are interspersed with large, peculiar and nearly pellucid cells. Its under part forms

a soft and delicate pad, or upper lip, and is continuous at the sides with the inferior half of the second segment, or under lip, to complete the oral orifice from which the mucous membrane of the mouth is reflected inwards. The mouth is a wide tube surrounded by a delicate muscular coat, and attached to the outer tube, or rings, by fine muscular bands. Behind, it dilates into a capacious heart-shaped sac, of which the roof or upper wall is covered by a thick oval muscular mass. The outer portion of this mass is divided into distinct, radiating, digital muscles which connect it on all sides and are continuous with the longitudinal muscles of the rings. Its inner surface projects anteriorly into the cavity of the pharynx, in the form of a thick circular disc or sucker, surrounded by loose folds of mucous membrane. Opening into the sides of the mouth and pharynx are two or three sets of salivary glands, which consist of convoluted tubules, resembling those of Lepidopterous insects: these glands have not been hitherto detected in *Lumbricus terrestris*. The pharynx contracts into a comparatively narrow œsophagus, which in its turn dilates into a capacious crop; and this immediately opens into a cylindrical gizzard composed of a ring of cartilage, with an external muscular coat, and a lining of mucous membrane. A long straight and narrow intestine extends through the rest of the body, and is covered throughout with yellow, follicular, hepatic glands in circles corresponding to the segments.

Nervous System.—The central organs of the nervous system consist chiefly of a bilobed cephalic ganglion, and a double chain of subventral ganglia extending through the whole length of the body. The lateral lobes of the cephalic ganglion are pyriform, and united by their broader ends in the mesial line. The small end of each divides into two nerve-trunks, of which one forms the root of its cephalic nerves, and the other, the pharyngeal crus, which curves round the side of the pharynx to join the first subventral ganglion. Each crus gives off eight or nine branches. The first four or five arise from the under part of its anterior half, and immediately enter the upper surface of a minute and delicate cord-like chain of ganglia, the enlargements of which correspond to them in number and size. This highly interesting structure lies on the side of the pharynx, concealed beneath the crus. The breadth of its first ganglionic enlargement in a good-sized worm, was the $\frac{1}{200}$th of an inch; that of the

last the $\frac{1}{130}$th; the pharyngeal crus, where their roots come off, was $\frac{1}{100}$th of an inch in diameter. Each border of the chain gives off several trunks of considerable size, which immediately communicate to form a continuous plexus. The part of the plexus on the inner side is much the larger, and supplies anteriorly, the muscular and mucous coats of the mouth as far as the lips; and posteriorly, the pharynx and suctorial disc; uniting in both directions with its fellow of the opposite side. The outer part supplies the muscular bands and salivary tubules. From the pharynx, the plexus descends along the side of the œsophagus, lying on the abdominal vessels, and communicates with minute filaments from the nerves of the subventral ganglia.

The whole of this little chain with a large portion of its plexus and the wall of the pharynx on which it lies, was removed and examined under a $\frac{1}{8}$th-inch object-glass, when a beautiful and unexpected appearance was observed. The under surface of the *entire* chain—cords as well as ganglia—was covered with a lamina of round, oval, and pyriform cells; and on its upper surface a row of cells of the same kind was found along each border. At every point of communication between the branches which form the plexus, a minute ganglionic enlargement was observed, from which new branches proceeded to form other enlargements of the same kind. Every branch communicated by loops with those adjacent, and by transverse fibres with those of the opposite side, giving to the ganglionic points a kind of stellate appearance. In these microscopic ganglia, the nerve-cells, similar to those of the chain, were accumulated chiefly about the angles, along the borders, and extended some distance into the principal trunks; but very few could be seen in connexion with nerve-fibres, which ran around and between them, however, in an intricate manner. As the plexus extended from the chain, the ganglionic points diminished in size, while the smaller branches given off from the trunks increased in number, and communicated like a capillary network. At the same time the ultimate fibres became paler, flatter, more parallel, and acquired nuclei like those of cells. This was particularly observed in those distributed to the mucous membrane. The above observations were repeated on nearly forty different specimens.

On considering the parts which it supplies, this little chain appears to combine the office of a sympathetic with certain other functions

which in many Invertebrata are entrusted to separate and special centres;—such as the labial, pharyngeal, and visceral ganglia in Cephalopodous and Gasteropodous Mollusca, and the separate parts of the stomato-gastric system of insects, which, although derived from different sources, are in intimate communication with each other. The lateral ganglia in insects have the same position as the little chain of *Lumbricus*, on the side of the pharynx, which, according to Mr. Newport, is supplied entirely by them; they arise, however, wholly from the cephalic ganglion, while the chain in *Lumbricus* has just been seen to take its origin both from this and the pharyngeal collar; but then, in orthopterous insects, the gangliated recurrent nerve, which is always in intimate connexion with the lateral ganglia, arises entirely from the pharyngeal crus; and the fact has been observed by Burmeister, Brandt and Müller, that in some other orders these two parts, in regard to size, are in the inverse ratio of each other. In Crustacea also, the whole of the pharyngeal, gastric and visceral nerves take their origin from the crura, as was first shown by Audouin and Milne-Edwards.

The second set of nerves from the pharyngeal collar come off from its posterior half, and communicate with each other by loops before they leave it. The first and largest sends some filaments to the muscular bands of the mouth, upon which they communicate by evident but slight dilatations with the plexus of the pharyngeal chain; and after supplying the muscles of the anterior segments, are lost in the integument of the lower lip. The rest take nearly the same course. But what is extremely interesting, the roots of this set—at least of the first and second branches—are continuous across the crus with those of the former set which belong to the pharyngeal chain; and many of their fibres may be traced not only into its ganglia, but through the trunks which proceed from their opposite sides to form the pharyngeal ganglionic plexus; so that the nerves distributed to the labial muscles and integument of the outer tube, and those which supply the inflected oral and pharyngeal tube, are in direct continuity, not only at their peripheral extremity, but at their roots also, through the common centre which presides over the whole of the digestive apparatus. A similar connexion will be seen to exist with regard to the cephalic nerves.

The subventral chain is a double cord gangliated at short intervals

by the addition of vesicular substance. Anteriorly the cords are separate and continuous with the pharyngeal crura of their respective sides; but through the rest of their course they lie in close contact along the middle line. The ganglionic enlargements vary somewhat in size, shape, and approximation at different parts. The vesicular substance is on their under surface, and consists of about two strata of cells continuous in a lamina across both cords. Along their borders, however, the cells form a thicker layer or column, which extends for some distance along the intervening cords. In form and general appearance the cells are similar to those of the pharyngeal chain, but many of them are larger. Those of the first ganglion extend into the lower parts of the crura, and are continuous behind with the lamina of the second. Each ganglion gives off from its sides two pairs of nerves, which, after sending some filaments to the septa and muscular bands, supply the longitudinal, oblique and circular muscles of the rings. Midway between the ganglia, the intervening cords give off a single pair, which are distributed to the deep muscles on each side. Within the ganglia the roots diverge in three different ways:—1, longitudinally; 2, transversely; and 3, to the grey or vesicular substance. The first or longitudinal form a large portion of the nerves, and run in equal numbers in both directions—backwards and forwards,—along the whole breadth of the corresponding cord. In their course, some of them, near the border, separate in succession from the rest and enter the lateral columns of cells; others proceed as far as the next nerve, with the roots of which they form loops, and pass out, while the rest continue onwards and, perhaps, in succession form similar loops with distant nerves. In former communications to the Royal Society, the author has shown that the same kind of arrangement exists in the spinal cord of Man and Mammalia.

The second or transverse order of fibres are less numerous, and in general less distinct than the last. They proceed from the middle of each opposite root, and cross the cords directly; but some of them, on reaching the opposite cord, turn round in both directions, and run with its longitudinal fibres. In front of the first ganglion, in which they are unusually distinct, a separate band unites the roots which descend from the branches arising from the opposite crura of the pharyngeal collar.

The third order of fibres, or those distributed to the vesicular substance, spread out in all directions, but always—except in the lateral layers or columns—beneath the superficial stratum. After nearly fifty separate examinations, with all the resources of the microscope, the author has not been able, in more than two or three instances, to trace an undoubted continuity between the cells and nerve-fibres. Fibres in abundance may be seen in connexion with the cells, but the greater number of these are not nerve-fibres. Nevertheless, there is reason to believe that such a connexion does frequently exist, but is obscured by certain peculiarities of structure. Still it is quite certain that a vast number of fibres pass by or around the cells near their origin, and many often appear to terminate in loops.

Cephalic Ganglion.—This rests on the commencement of the pharynx, beneath the dorsal part of the third ring. Each lobe is a pyriform sac, which is very thick and convex posteriorly, where it is partially separated from its fellow by a deep notch. This convex portion is opaque-white, and filled with a mass of semifluid granular substance, and oval, round and pyriform cells, of various sizes, but often very large. Some of the latter kind are exceedingly elongated. The anterior half, by which the lobes are joined, is merely *lined* with a *lamina* of cells, and only at its upper part, its under side having a cell here and there. The *interior* of this portion is entirely *fibrous*, and consists of a broad transverse commissural band derived from the pharyngeal collar, and of fibres from the roots of the cephalic nerves. Each crus of the collar enters its lobe on the *under* side. Some of its fibres curve backwards to the convex vesicular mass; others ascend to—perhaps partly terminate *in*—the cells near the roots of the cephalic nerves; and the rest cross transversely as the broad band, to be continuous in front of the notch with that of the opposite crus. The cephalic nerves are attached to the *upper* part of the ganglion. Many of their roots cross transversely with the crural band, to form loops with those of the opposite lobe. Decussating these, a considerable number run down the pharyngeal crus, and enter the pharyngeal chain of ganglia through its first and second roots, at least,—perhaps through all,—and probably form loops with the other set of branches of the crus. The remaining fibres of the cephalic nerves spread through the vesicular substance, partly describing curves and undulations in the corresponding lobe, and com-

municating in part with the other in the mesial line, where they form a kind of indistinct decussation in front of the notch.

Distribution of the Cephalic Nerves.—Their roots on each side immediately separate into two trunks, a lower and upper. The former runs above the mouth, to the under side of the first conical segment, or upper lip. Here it divides into several branches, which supply its muscular bands, and then terminate in the integument as a plexus, which appears to communicate with that from the first enlargement of the pharyngeal chain, spread over the tubular mouth, which is itself continuous with the upper lip. The upper trunk proceeds directly to the corresponding part of the same segment, and there divides into two branches, of which one in particular, after running the course of the pigmentary laminæ, and giving off a series of short filaments, terminates at the point, beneath the integument.

In the pigmentary laminæ the nerves form an intricate plexus, and the impression was that many of their ultimate fibres end in loops. They were never seen to be directly connected with the large clear cells scattered through the substance. Nor is there any ground for conjecture with regard to the office of these cells: perhaps they are intended for the transmission of light. From the structure of the segment and the distribution of its nerves, it is not unreasonable to think that its upper surface may be instrumental in the perception of diffused light; and that its under surface and point may be subservient not only to the sense of touch, but perhaps also to that of smell, in a low degree. That it forms an important organ of search, is pretty evident from the manner in which it is projected alternately forwards and from side to side, as the animal advances in its course.

The upper side of the cephalic ganglion corresponds to the under side of the subventral, and several points of resemblance are pointed out between the two kinds of centres. Each pharyngeal crus is shown to be a compound structure, composed of different sets of connecting fibres,—1, between its own nerves, which supply, on the one side, the cephalic portion of the outer tube, and on the other, the corresponding part of the alimentary tube reflected inwards from the former; 2, between these nerves and their fellows of the opposite crus, across the front of the first ganglion; 3, between the same nerves and the cephalic ganglion; and 4, between the cephalic

ganglion and the same side of the whole subventral chain. Now there is this point of *difference* between the two kinds of centres compared together,—that while the last-mentioned set of fibres on the one side is continuous with that on the other, as a transverse band through the cephalic ganglion, the subventral cords, although continuous with these on their respective sides, form no such connexion with each other across the lateral halves of their own ganglia, but run parallel and directly *backwards* through them. Such a communication, however, is established for the latter, individually, by the transverse fibres of their *own nerves*; and just as these fibres unite the lateral halves of each *separate* ganglion, *independently of the cephalic*, so do the last-mentioned set of fibres of the crura connect together the two lateral halves of the *entire chain in* and *through* the cephalic ganglion, which is their dominant and controlling centre.

Two parts of the human brain may be compared to this transverse cephalic band. One is the arched and commissural band of fibres prolonged through the corpora quadrigemina, from the upper and inner part of the fillet on each side. But the outer part of the fillet turns forwards and upwards beneath the corpus geniculatum internum and optic tract, to enter the optic thalamus. It is not improbable, therefore, that some of the fibres of the tract may descend along this portion of the fillet, to form loops with the roots of the fifth nerve, over which it passes, since in *Lumbricus* it has been seen that many of the roots of the cephalic nerves run down the pharyngeal crus to form loops with others to which it gives origin. In a former memoir by the author, it was shown that some of the roots of the spinal accessory nerve reach the anterior grey cornu and mingle, perhaps pass out with, the spinal roots; and he has since observed the equally interesting fact, that the same nerve forms a similar connexion with the vesicular nucleus of the hypoglossal, which may be considered a representative of the anterior spinal. The spinal-accessory, therefore, takes it origin from at least three different sources,—from its own nucleus, and from the nuclei of the hypoglossal and anterior spinal nerves. The peripheral communications of both the former with the latter nerves in the cervical plexus is well known. The author believes he has also made out an intimate connexion by loops between at least the portio intermedia of the

seventh and the large root of the fifth nerves within the substance of the human medulla.

The other part of the human brain which is analogous, or homologous with the cephalic band of *Lumbricus*, is the corpus callosum. Gall and others have thought that the fibres of this structure arise from the grey substance of the hemispheres; while some have endeavoured to show their continuity with those of the crura cerebri. Now it is quite certain that in the cephalic ganglion of *Lumbricus*, a large proportion of the commissural fibres are directly continuous with those of the pharyngeal crura; and there are appearances which favour the conclusion that some of the latter are confined to the lobe on their own side. From *analogy*, then, we may infer, that while a large portion of the crura cerebri are directly continuous with the corpus callosum, some of their fibres *probably* terminate in the cerebral convolutions of the corresponding side.

From what has been shown, it is evident that the communications between the roots of nerves are more intimate and extensive than they were hitherto believed to be; for it has been seen that the roots not only of every spinal nerve, but of every other in the system, communicate with those which *correspond* on the *opposite*, and with those which are *adjacent* on the *same* side. Of the cephalic with the two sets from the pharyngeal collar, and of the latter with each other, the connexions are particularly interesting, and may serve as guides to future investigations on other forms of the nervous system.

By experiments that were made on the living worm, it is shown that the pharyngeal chain of ganglia are independent of the other nervous centres, although subject to their influence, and are not only competent of themselves to preside over the complicated movements of the suctorial pharynx and mouth, but appear also to be centres of reflex action.

The present memoir concludes with some observations and remarks on the ganglionic cords of other Invertebrata.